Universidade de Aveiro Departamento de Biologia
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Alvim Pereira
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Environmental drivers reveal fragmented spatial patterns of Eurasian badger (*Meles meles*) occurrence in Portugal

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Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ecologia Aplicada, realizada sob a orientação científica do Doutor Carlos Manuel Martins Santos Fonseca, Professor associado com agregação do Departamento de Biologia da Universidade de Aveiro e com orientação da Doutora Clara Bentes Grilo, investigadora de pós-doutoramento da Universidade Federal de Lavras (Brasil).

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agradecimentos

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palavras-chave

texugo, texugueira, atropelamentos, modelação de habitat, distribuição, conservação

resumo

Perceber os fatores ambientais que influenciam a ocorrência e distribuição de espécies é essencial para a formulação de medidas de conservação eficientes. O texugo Europeu (*Meles meles*) é um dos carnívoros mais comuns nos ecossistemas Mediterrânicos mas o aumento da fragmentação de habitat nas últimas décadas pode originar uma mudança no seu estatuto e distribuição. A sua ampla distribuição geográfica juntamente com o facto de ser uma espécie generalista em termos de habitat e alimentação torna difícil encontrar um padrão de seleção de habitat único. Neste estudo foram analisados os factores ambientais que influenciam a localização das tocas (vulgarmente conhecidas como texugueiras e usadas para reprodução e refúgio), a ocorrência de texugo e o risco de atropelamentos. O principal objectivo é avaliar os padrões espaciais de habitats de alta qualidade e de alto risco para a conservação do texugo em Portugal. Prospetámos o centro de Portugal à procura de texugueiras e compilámos os dados de ocorrência de texugo e de atropelamentos a nível nacional. Usámos modelos lineares generalizados (GLM) para examinar os fatores que influenciam a localização das texugueiras e modelos de entropia máxima (MaxEnt) para analisar o que leva à ocorrência de texugo e à sua mortalidade nas estradas. Por fim, os três modelos foram sobrepostos com o objetivo de identificar áreas prioritárias para a conservação do texugo. Os nossos resultados revelaram uma fragmentação no padrão espacial dos habitats primários. Surpreedentemente, o texugo evita áreas densamente florestadas para a seleção do local das texugueiras e a sua ocorrência está positivamente relacionada com a presença de alguma proporção de campos agrícolas, solos sedimentares e áreas abertas. O risco de atropelamento é mais elevado em autoestradas com sinuosidade baixa e perto de zonas abertas. Os nossos resultados realçam a importância da manutenção de florestas Mediterrânicas naturais, pastos e zonas agrícolas. Deve ser dada prioridade às zonas de alto risco em termos de investigação (validar os resultados com uma estimativa das taxas de atropelamentos) e conservação (incluir passagens para minimizar o número de atropelamentos). É necessário mais investigação para determinar se as áreas de habitat primário disponíveis têm algum efeito na viabilidade das populações de texugo ao longo do tempo.

keywords badger, badger sett, road mortality, habitat modelling, distribution, conservation

abstract

Understanding the environmental features that influence organism's occurrence and distribution is essential to formulate efficient conservation measures. The European badger (*Meles meles*) is one of the most common carnivores in Mediterrranean environments but the increase of habitat fragmentation over the last decades may lead to a change in their status and distribution. Badger have an wide geographic distribution and together with the fact that are generalist in terms of habitat and food makes it difficult to find a unic habitat selection pattern. In this study we address to analyse the environmental drivers that influence the location of badger setts (used for reproduction and refuge), the occurrence of badgers and their risk of road mortality. The main goal of this study is to evaluate the spatial patterns of habitats of high quality and high risk for badger conservation in Portugal. We surveyed the centre of Portugal in search of badger setts and compiled badger occurrence and road-kill data at a national level. We used generalized linear modelling (GLM) to examine which factors influence the badger sett sites and maximum entropy modelling (MaxEnt) to analyse the drivers of badger occurrence and road mortality. Finally, we overlapped the three models to identify priority areas for badger conservation. Our results reveal a fragmented pattern of primary habitats for badgers. Surprisingly, when selecting the location of badger setts they seem to avoid densily forested areas and their occurrence is positively related to some amount of agricultural fields, sedimentary ground and open areas. Road mortality risk is high at highways with low sinuosity and close to open areas. Our results highlight the importance of the mantainance of natural Mediterranean forests, pastures and some agricultural lands. Priority should be given to risky areas in terms of reasearch (by validating the results with the estimation of road-kill rates) and of conservation (inclusion of crossing structures to minimize the number of road-kill events). Further research should be performed to determine whether the available primary habitat have an effect on populations viability over time.

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The European badger (*Meles meles* L., 1758) is a social mammal that frequently live in groups, with several individuals often sharing the same territory (Rosalino 2004). This medium sized carnivore has an extensive geographic distribution, ranging from the British islands to Turkey (Proulx and Do Linh San 2016) and their conservation status is of Least Concern in Europe (The IUCN Red List of Threatened Species; Kranz *et al.* 2016) and also in Portugal (Portuguese Red Book of Vertebrates; Cabral *et al.* 2005). Badger ecology and habitat selection is a very studied topic but most of the information are from northern Europe, mainly United Kingdom (where they occur in high population densities; Neal 1972), lacking information in Mediterranean areas. In Portugal there is few studies on the south, being the national distribution unknown.

Badgers have very different social organizations and different habitat preferences over their distribution range (Rosalino 2004). This results in a variability of home range sizes, being relatively large in Portugal (4.46km^2; Rosalino 2004) compared to United Kingdom (0.14km^2; Cheeseman *et al.* 1981) but small compared to other European regions (e.g. 24.4km^2 in Poland, Kowalczyk *et al.* 2003). In Portugal their presence is usually in low densities (Revilla *et al.* 2000; Rosalino 2004) which makes them particularly vulnerable to habitat fragmentation and road traffic (Seiler *et al.* 2003). This predator builds complex tunnel systems under the ground, which provide shelter and may be used for breeding, known as badger setts (Neal and Cheeseman, 1996; Rosalino 2004). These setts usually have a main sett (several entrances, used most of the year) and secondary setts (smaller, occasionally used) (Jepsen *et al.* 2005). Due to reproduction and food availability they often change setts in a dispersal process that is done progressively over several months (Roper *et al.* 2003; Rosalino 2004). Badgers are often described as generalist in terms of food and habitat (Roper 1994; Neal and Cheeseman 1996; Revilla and Palomares, 2002; Virgós 2002) and opportunistic, with their diets varying according to food availability (Kruuk and Parish 1981). In Portugal and Mediterranean areas, it is believed that they eat mainly fruit and insects

(Rosalino *et al.* 2005a; Barea-Azcón *et al.* 2010), while in northern European areas their favourite food component is earthworms (Kruuk *et al.* 1979; Hammond *et al.* 2001; Zabala *et al.* 2002; Elliott *et al.* 2015).

Regarding the choices of habitat, local features are considered more important to the selection of badger sett sites (Jepsen *et al.* 2005) while larger-scale characteristics are more important to badger habitat selection and occurrence. Geological features that facilitate the construction of setts and proximity to food or water are some of the most important local features that limit the selection of sites for construction of badger setts (Rosalino 2004; Jepsen *et al.* 2005). Because of their wide distribution with ecological differences between populations, studies on badger habitat selection show a high diversity of land use features preferences (da Silva *et al.* 1993; Brøseth *et al.* 1997; Feore and Montgomery 1999; Revilla *et al.* 2000; Rosalino *et al.* 2005b; Lara-Romero *et al.* 2012). In Europe, deciduous forests are usually considered the most important habitat for badgers (Neal 1972; Van Apeldoorn *et al.* 1998; Wright *et al.* 2000; Rosalino 2004; Santos and Beier 2008), but also orchards (Lara-Romero *et al.* 2012), pastures (Hammond *et al.* 2001; Zabala *et al.* 2002) and shrubs (Rosalino *et al.* 2007; Lara-Romero *et al.* 2012). Deciduous forests provide favourable soil for sett construction (Kruuk and Parish 1981), cooler climate during summer, secure shelter for movements between patches and stable food availability (Rosalino *et al.* 2004, 2007). Orchards and pastures provide food while shrubs provide shelter and may be used as resting sites (Rosalino *et al.* 2007).

Road-kills are one of the main causes of mortality of badger populations in most of their distribution range. The effects of roads on wildlife has been increasingly studied in the last years due to the rapid road expansion (Pertoldi *et al.* 2001) and greatly depends on the species perception of risk and on their life history traits, with some species being more vulnerable than others (Gunson *et al.* 2011). Some species seem to perceive better the risk of road crossing and avoid them, as is the case of weasels (Grilo *et al.* 2008, 2009). That is not the case of badgers, that may travel long distances looking for food patches (Rosalino 2004), which raises the probability of encountering roads and collide with a vehicle (Alexander *et al.* 2005).

Furthermore, they are also more vulnerable to traffic during breeding and dispersal periods, which may affect the next generations (Grilo *et al.* 2009).

Due to the great diversity of ecological aspects between European populations and to their generalist habits, it’s difficult to find distribution and habitat selection patterns. Understanding the environmental features that affect the presence of badgers at a national level is essential to better comprehend the species ecology requirements and to formulate efficient conservation measures.

Environmental drivers reveal fragmented spatial patterns of European badger (*Meles meles*) occurrence in Portugal

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Abstract

Understanding the environmental features that influence organism's occurrence and distribution is essential to formulate efficient conservation measures. The European badger (*Meles meles*) is one of the most common carnivores in Mediterranean environments but the increase of habitat fragmentation over the last decades may change their status and distribution. The main goal of this study is to evaluate the drivers and spatial patterns of high quality and high risk for badger conservation in Portugal. We surveyed the centre of Portugal in search of badger setts and compiled badger occurrence and road-kill data at a national level. We used generalized linear modelling (GLM) to examine which factors influence the location od badger setts and maximum entropy modelling (MaxEnt) to analyse the drivers of badger occurrence and road mortality. We combined the badger setts likelihood, badger probability of occurrence and road mortality risk to identify primary habitat and primary risky areas. Our results reveal a fragmented pattern of primary habitats for badgers. Surprisingly, badgers avoid forested areas for the selection of sett sites. Some amount of agricultural fields, sedimentary ground and open areas seem to be favourable for their occurrence. Road mortality risk is high at highways with low sinuosity and close to open areas. Our results highlight the importance of the mantainance of natural Mediterranean habitats and some agricultural lands for the persistence of badger populations. Further research is needed to determine whether the available primary habitat have an effect on populations viability.

Keywords

badger, badger sett, road mortality, habitat modelling, distribution, conservation

1. INTRODUCTION

Understanding the environmental features that influence organism's occurrence and distribution is a fundamental topic in conservation biology (Gaston and Blackburn 1999; Guisan and Zimmermann 2000). Species distribution range is often associated to extinction risk. Thus, identifying the main factors that limit the species occurrence and map favourable areas within species range is essential to assess its conservation status and formulate efficient conservation measures when needed (Pompa *et al.* 2011; Marcer *et al.* 2013; Fourcade *et al.* 2014).

However, information from systematic surveys is scarce for the majority of the species (Newbold 2010). Occurrence data from opportunistic observations is the most common source of information (Marcer *et al.* 2013). In order to deal with these limitations, statistical modelling has been increasingly used to understand how certain environmental features affect species habitat selection and distribution (e.g. Naves *et al.* 2003; Marcer *et al.* 2013).

The European badger (*Meles meles* L., 1758) is one of the largest mustelids in Europe and has an extensive distribution, ranging from the British islands to Turkey (Proulx and Do Linh San 2016). Mainly because of its wide distribution, badger is listed as Least Concern in Europe (The IUCN Red List of Threatened Species; Kranz *et al.* 2016) and also in Portugal (Portuguese Red Book of Vertebrates; Cabral *et al.* 2005). Badger habitat selection over Europe show a high diversity of land use preferences (da Silva *et al.* 1993; Brøseth *et al.* 1997; Feore and Montgomery 1999; Revilla *et al.* 2000; Rosalino *et al.* 2005b; Lara-Romero *et* *al.* 2012). In Mediterranean environments there are three general drivers that define occurrence of badger populations: 1) the territory range is influenced by the dispersion of food patches, 2) the number of individuals per group is affected by the availability of food sources and 3) the location of badger setts is determined by the presence of geological features (Rosalino *et al.* 2005b). Nevertheless, the habitat fragmentation and isolation due to urbanization in the last decades (Pertoldi *et al.* 2001; Rosalino 2004) may put at risk the persistence of badgers in some areas. Moreover, the expansion of road network has increased the non-natural mortality rates due to badger-vehicle collisions (Pertoldi *et al.* 2001; Grilo *et al.* 2009). For some species, roads can become ecological traps when overlap highly suitable habitats (Naves *et al.* 2003; Northrup *et al.* 2012a, b). In Sweden and Netherlands badgers have increased losses (10-20%) due to road traffic (Seiler *et al.* 2003; Dekker and Bekker 2010). In southern Portugal the estimated road-kill rate was 5 ind./100km/year with peaks of mortality during breeding and dispersal periods which may put at risk the next generation (Grilo *et al.* 2009).

Studies on habitat selection are usually one-dimensional (the majority based on locations) which is insufficient since the species occurrence is also related with species mortality risk (Naves *et al.* 2003). Therefore, it is crucial to use different data types from different bio-ecological features to provide valuable information on species spatial patterns: setts location and suitable habitat areas may indicate the location of source patches and areas with high mortality risk may reveal sink areas (Pulliam 1988; Battin 2004). In the absence of demographic parameters that can evidence source and sink patches, spatial models that predict occurrence and mortality can provide valuable insights to define priority areas for species conservation (Naves *et al.* 2003; Roever *et al.* 2013). In Portugal the information on the environmental features that lead to the location of badger setts, the patterns of badger occurrence and distribution and the areas with higher mortality risk at a large scale is scarce.

The main goal of this study is to evaluate what are the spatial patterns of high quality and high risk areas for badger conservation in Portugal. In more detail, this study aimed to: 1) analyse the factors that explain the occurrence of badger setts, badger presence and road mortality risk at a national level; and 2) identify primary habitat areas (areas with high likelihood of badger setts and badger occurrence and low risk of road mortality) as well primary risk areas (areas with high likelihood of badger setts and badger occurrence and road segments with high risk of badger mortality).

We compiled badger data (badger setts, occurrences and road-kill events) and analysed in terms of landscape and human pressure variables. We used generalized linear modelling (GLM) to examine which factors affect the occurrence of badger setts and maximum entropy modelling (MaxEnt) to identify which factors explain badger occurrence and road mortality. Finally, the three models were combined to define priority areas for badger conservation.

2. METHODS

2.1. STUDY AREA

All analysis of badger setts, badger occurrence and mortality were run for the continental Portugal (Fig. 1). The predominant land use type in Portugal is forest (35%) followed by shrubs and pastures (32%) and agricultural fields (24%) (CELPA 2015). The most common forest type is eucalyptus (*Eucalyptus globulus*) and pine (*Pinus pinaster*) plantations that occur mostly at the north and centre of Portugal (CELPA 2015). Cork woodlands (*Quercus suber*) dominate southern Portugal. Over the country we can also find patches of common oak woodlands from different species (*Quercus robur, Quercus pyrenaica, Quercus faginea, Quercus ilex*) (CELPA 2015). The climate is mainly associated with the Mediterranean region which correspond to dry hot summers and cold rainy winters (IPMA 2016). Portugal has a mean population density of 112 ind./km^2 (INE 2015) mostly concentrated in the coastline and an average road density of 0.2 km/km^2 (IMT 2014).

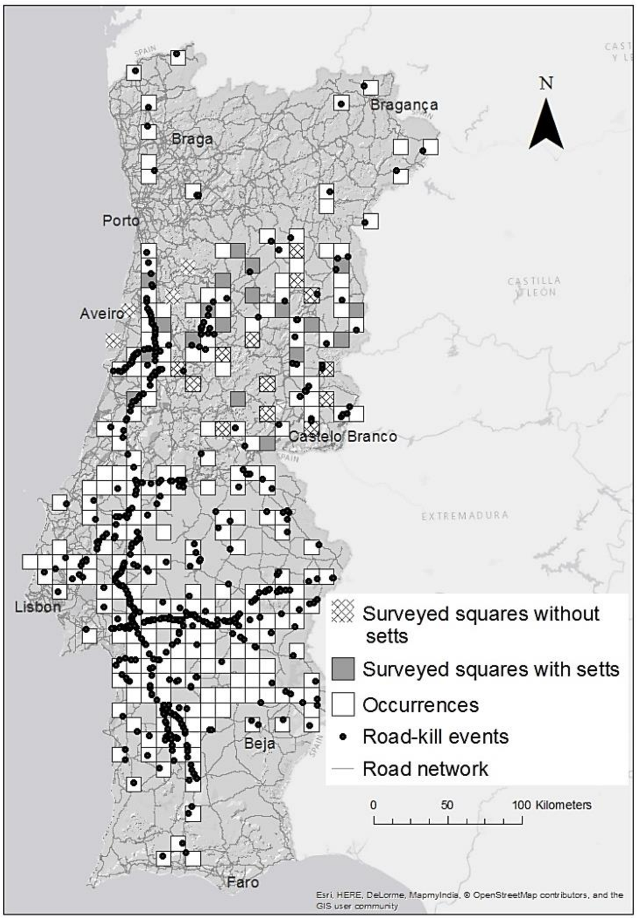

Fig. 1 Study area with surveyed squares with and without badger setts, badger occurrence data, badger road-kill events, road network and main cities

2.2. DATA COMPILATION

2.2.1. Badger setts survey

The badger setts survey was performed in the scope of the 1st Iberian Badger Survey *(I Sondeo Iberico de Tejoneras)* promoted by the Group of Terrestrial Carnivores of the Spanish Society for Conservation and Study of Mammals (SECEM – *Sociedad Española para la Conservación y Estudio de los Mamíferos*). The fieldwork was carried out between May 2014 and November 2015 with a two-people team in search of badger setts. We surveyed 36 squares of $10x10km^2$ previously selected in a systematic approach (see details in http://iberianbadgersurvey.blogspot.pt/). In each square of $10x10km^2$ we selected two squares of $5x5km^2$ of each we performed five transects of 500m (randomly selected) separated by at least 500m. We recorded the coordinates of all badger setts.

2.2.2. Badger occurrence and road-kill data compilation

We compiled badger presence data in continental Portugal (Fig. 1). The data was from different sources and included: badger setts, tracks (footprints), scats (latrines), direct observations, camera trap photographs, observed dead individuals and road-kill records. Badger setts and others signs of badger occurrence (setts, latrines and tracks) were obtained from the 1st Iberian Badger Survey (2014-2015) in Central Portugal (see badger setts survey); the others types of badger data (tracks, scats, dead individuals, direct observations, camera trap photographs) were obtained from Grilo *et al.* (2008), University of Aveiro/UVS, CERVAS/Aldeia and personal observations. Road-kill data was obtained from Grilo *et al.* (2009), Brisa Auto-estradas de Portugal (Grilo and Santos-Reis 2009) and Infraestruturas de Portugal, SA management (Grilo and Santos-Reis 2014). The data were assigned to a grid square of $10x10km^2$ covering all national territory in terms of presence-only data. To estimate the badger-vehicle collision risk, we assigned the road-kill records to each road segment of 500m.

2.2.3. Environmental variables compilation

We defined a grid of $500x500m^2$ to describe in terms of presence/absence of badger setts (used and unused) and 13 variables related with the importance for badger sett construction (Annex – Table A). The variables were divided in three main categories: 1) landscape (open areas, permanent cultures, temporary cultures, heterogeneous agricultural areas, forests, arboreal cover and distance to streams), 2) soil type (sedimentary ground, metamorphic/ sedimentary ground, igneous plutonic ground and floodable soil) and 3) human pressure (population density and distance to roads) (Annex – Table A).

We defined a grid of 10x10km^2 to describe in terms of presence of badger and 16 environmental variables considering their importance for badger species occurrence in literature (Annex – Table B) (e.g. Krebs 1994; Huck *et al.* 2008). The variables encompassed five categories: 1) topography (altitude); 2) climate (precipitation, temperature and humidity); 3) land use (urban areas, open areas, permanent cultures, temporary cultures, water bodies, heterogeneous agricultural areas and forests); 4) soil type (sedimentary ground, metamorphic/ sedimentary ground, igneous plutonic ground and igneous volcanic ground); and 5) human pressure (population density) (Annex – Table B).

We defined a grid of 500x500m^2 for the road network and included information of presence of road-kill events and 12 environmental variables to estimate the road mortality risk (Annex – Table C). The variables were divided in three categories: 1) road-related (type of road, number of intersections river-roads and road sinuosity (calculated by the fraction of the road length by the shortest path length)); 2) landscape connectivity (distance between patches of the same land use class that are crossed by the road: urban areas, open areas, permanent cultures, temporary cultures, water bodies, heterogeneous agricultural areas and forests) and landscape diversity (calculated through the Shannon-Weiner index); and 3) human pressure (population density) (Annex – Table C).

All spatial analysis were performed with the ArcGIS 10.2.2 software (ESRI, Redlands, USA).

2.3. DATA ANALYSIS

2.3.1. Factors affecting the occurrence of badger setts

We used Generalized Linear Model (GLM) to analyse the occurrence of the badger setts. We used a binomial distribution and a logit link with the sett and non-sett points as the response variable (1 - sett, 0 - non-sett). We used all setts found in the field and non-sett locations randomly obtained within the surveyed squares in a proportion of 40 and 60%, respectively.

We designed 23 candidate models to explain the occurrence of badger setts, assuming four groups of hypothesis and taking into account the 14 variables: 1) landscape features that represent food and shelter availability explain badger sett occurrence, 2) the type of soil affect the selection of setts, 3) low human pressure explain the badger sett occurrence, or 4) the combination of landscape, soil type and human pressure features explain the occurrence of badger setts. For each group of hypotheses, we run a model with all combination of variables. Afterwards, we run all combinations of the best models of each group of hypotheses. All models were ranked according to Akaike's Information Criterion (AIC) (Akaike 1983). We decided to use the second-order Akaike's Information Criterion (AIC_c) that is transformed for small sample sizes and compared models based on the Akaike weight (w_i) (Burnham and Anderson 2002). We tested multicollinearity with the Pearson coefficient criteria and did not enter in the same model correlated variables (higher than ±0.5) (as suggested by Booth *et al.* 1994). If more than one model had $\Delta AIC_c \leq 2$ (with similar good performance) we performed model averaging to produce a model average prediction of badger setts (Burnham and Anderson 2002). Statistical modelling procedures were carried out with R 3.2.4 software (R Development Core Team, 2016).

2.3.2. Factors affecting the occurrence of badgers

We performed the Maximum Entropy Modelling of Species Geographic Distributions method, also known as MaxEnt, version 3.3.3k (http://www.cs.princeton.edu/~schapire/maxent; Philips *et al.* 2011) to estimate the likelihood of badger occurrence. This method compares the georeferenced presence data of the species (response variable) with the selected environmental layers (explanatory variables) of the study area (Philips *et al.* 2006; Kumar and Stohlgren 2009; Elith *et al.* 2011). Then it estimates the species probability of occurrence based on an extrapolation of suitable habitats using a logistic transformation of suitability index of all study area (Philips and Dudik 2008; Royle *et al.* 2012). This prediction is performed by incorporating the minimum amount of information as input data, therefore it only uses non-systematic presence-only data (Convertino *et al.* 2014). It gives us an estimate probability of the species presence in a value between 0 and 1, being 0 the weakest probability and 1 the strongest. We used for training 80% of badger's data and 20% of the sample records for testing. Before running the model, we tested for correlation with the Pearson coefficient criteria between pairs of environmental variables and when a pair showed correlation (higher than ±0.9; as suggested by Fourcade *et al.* 2014), we selected the variable that most explain the badger occurrence.

Some regions of Portugal were unequally sampled which may make the occurrence of data biased in the geographical space and can lead to incorrect model predictions (Fourcade *et al.* 2014). Therefore, we included in the model a bias grid file (Elith *et al.* 2010; Merow *et al.* 2013; Fourcade *et al.* 2014). We produced the bias grid by deriving a Gaussian kernel density map of the occurrence locations with a radius of 20 km (10 times the average badger home-range radius in Portugal; Rosalino 2004). A high weight was assigned to badger occurrence points with fewer neighbours in geographic space and the grid was rescaled between 1 and 20 (see Elith *et al.* 2010). All statistics procedures for estimate the bias grid were performed in ArcGIS 10.2.2 (ESRI, Redlands, USA).

We used the logistic threshold of equal training sensitivity and specificity to map the probability of badger occurrence.

2.3.3. Factors affecting the badger road-kill events

We performed the Maximum Entropy Modelling of Species Geographic Distributions method to estimate the road mortality likelihood of badgers, as performed in the previous model for badger occurrence. We tested for correlation between environmental variables following the same approach for the occurrence model (Fourcade *et al.* 2014). Survey effort was included in the model through the bias grid that considered 84 months of survey of Brisa highways and 45 months for roads under Infraestruturas de Portugal, SA management. Model analysis and evaluation took the same procedures of the previous model for badger occurrence.

2.3.4. Spatial patterns of primary habitat and primary risk

We overlapped the three maps of badger setts likelihood, badger probability of occurrence and badger mortality risk to identify areas of primary habitat and primary risk for badgers. We defined primary habitat the areas with high badger setts likelihood, high probability of badger occurrence and low mortality risk. Primary risk areas were considered those areas with high badger sett likelihood, high probability of badger occurrence and road segments with very high mortality risk (see Roever *et al.* 2013). All spatial procedures were performed in ArcGIS 10.2.2 (ESRI, Redlands, USA).

3. RESULTS

3.1. Factors affecting the occurrence of badger setts

We found 30 badger setts which was approximately 0.17 setts/km. The 30 badger setts had a total number of 80 entrances, in which only four were active. In average, we found 2.5±1.6 entrances per badger sett, and some of them were probably secondary sett (with only one or two entrances) while others were clearly main setts (with three or more entrances). Around 39% of entrances of the setts were orientated to Northeast, 22% to Southwest, 20% to Southeast, and 19% to Northwest.

We found three pairs of variables with high correlation: forests/ permanent cultures, heterogeneous cultures/ arboreal cover, forests/arboreal cover and sedimentary ground/ igneous plutonic ground. For each candidate model, we selected the correlated variable with higher correlation with badger sett occurrence (Zuur *et al.* 2009).

We found eight models with $\Delta AIC_c \leq 2$ that included landscape, soil type and human pressure variables (Annex – Table D) and performed a full averaging model (Burnham and Anderson 2002; Symonds and Moussalli 2011).

The averaged model resulted in 65% of correct classifications (50% of correct presences and 80% of correct absences) and included six variables. The only significant variable was the arboreal cover, that had a negative association with badger setts likelihood (Table 1). Although the remaining variables were not significantly correlated with the badger setts likelihood, we found positive correlation with badger setts for temporary cultures, igneous plutonic ground, distance to streams and distance to roads and negative relation with open areas.

Table 1 Estimated coefficients (β), 95% confidence interval (CI), Z-test (z-value) and significance (p-value) for the averaged model of the GLM analysis of badger setts

Variables	**β**	**95% CI**		**z-value**	**p-value**
		min	max		
(Intercept)	0.06126	-0.96234	1.08486	0.14156	0.76469
Arboreal cover	-0.02234	-0.03979	-0.00489	-2.53639	0.01626
Temporary cultures	0.00981	0.00697	0.01266	1.33461	0.04920
Distance to streams	0.00023	-0.24310	0.24356	-1.34635	0.12503
Open areas	-0.06372	-0.30075	0.17332	0.49501	0.07991
Igneous plutonic ground	0.00104	-0.65531	0.65740	-0.25720	0.06916
Distance to roads	0.00008	-0.10170	0.10186	-1.21705	0.03937

To calculate and map the probability of badger setts occurrence we applied the formula of the averaged model:

Averaged model = 0.06126 + (-0.02234) x Arboreal cover + (-0.06372) x Open areas + (0.00981) x Temporary cultures + (0.00104) x Igneous plutonic ground + (0.00023) x Distance to streams + (0.00008) x Distance to roads

The threshold used to map the badger setts likelihood was the fixed value for GLM analysis (0.5). We defined three classes to map the probability: 1) below the threshold (<0.5), 2) the mean value between the threshold and the maximum value (0.5 – 0.731) and 3) above that mean value (>0.731) (Fig. 2a).

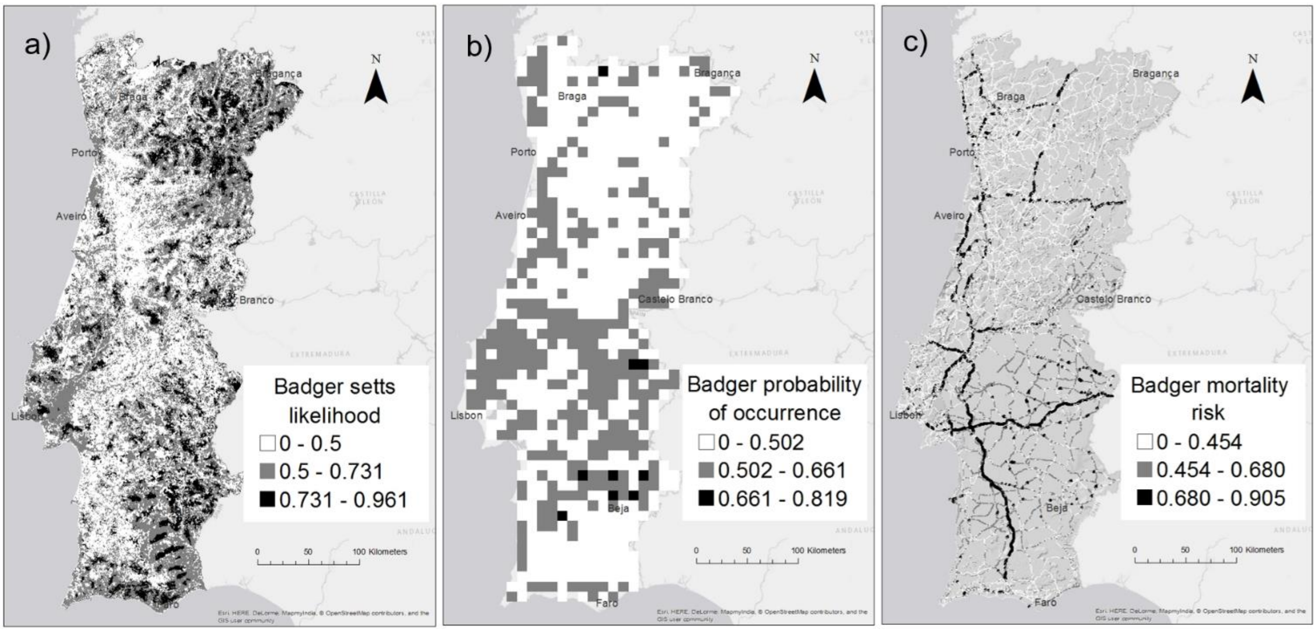

Fig. 2 Representation of the three models of: a) badger setts likelihood, b) badger probability of occurrence and c) badger mortality risk, and corresponding probability values

3.2. Factors affecting the occurrence of badgers

We obtained 282 squares of 10x10km^2 with badger occurrence data. The badger road-kill events were present in 224 squares, badger setts in 28 squares and others data types (tracks, scats, dead individuals, direct observations and camera trap photographs) in 88 squares (Fig. 1). We used 222 presences for model training and 55 for testing.

The final model produced a training data AUC of 0.7 which show a good performance and a good description of badger distribution (Elith *et al.* 2011).

The variables with higher contribution for badger's occurrence were (Table 2): permanent cultures (20.6%), sedimentary ground (15.5%), temporary cultures (11.7%), followed by open areas (7.6%), forests (5.8%) and igneous plutonic ground (5.1%).

Table 2 Percentage contribution of each environmental variable to the models of badger occurrence and badger mortality

Badger occurrence variables contribution (%)		**Badger mortality variables contribution (%)**	
Permanent cultures	20.6	Road type	41.6
Sedimentary ground	15.5	Road sinuosity	31.5
Temporary cultures	11.7	Distance to open areas	15
Open areas	7.6	Distance to water bodies	3.1
Forests	5.8	Distance to forests	2.7
Igneous plutonic ground	5.1	Distance to permanent cultures	2.5
Altitude	5	Distance to urban areas	1
Water bodies	5	Distance to heterogeneous agricultural areas	0.9
Metamorphic and sedimentary ground	4.7	Distance to temporary cultures	0.9
Heterogeneous agricultural areas	4.6	Landscape diversity	0.6
Human population density	4	Intersections river-roads	0.2
Igneous volcanic ground	3.9	Human population density	0.1
Humidity	2.8		
Urban areas	2.1		
Temperature	1.3		
Precipitation	0.2		

A high proportion of permanent cultures (>60%) was negatively associated with badger presence. The sedimentary ground had a slight positive relation with badger presence while temporary cultures had only a positive relation with the badger presence until a proportion of around 70% of the area. The open areas had a straight positive relation with badger presence. On the other side, the presence of forests had a straight negative relation with badger probability of occurrence. The igneous plutonic ground seemed to have a negative selection by badger (Fig. 3).

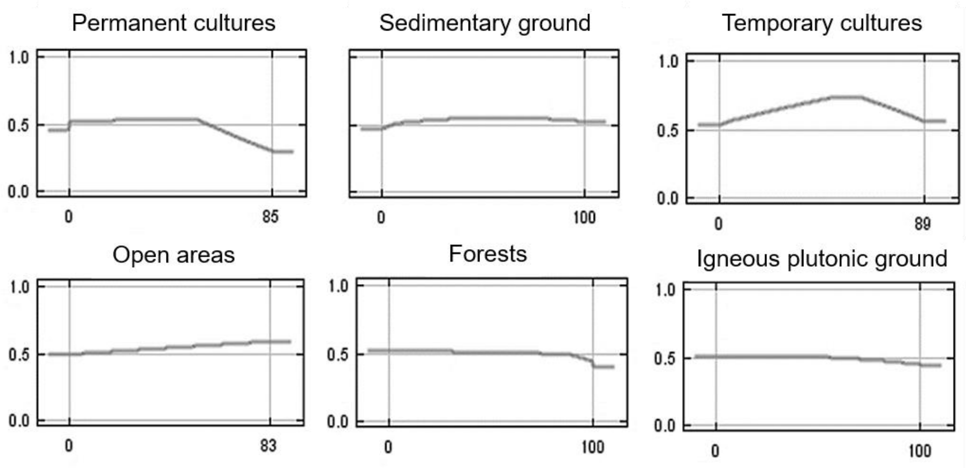

Fig. 3 Relationship between badger occurrence and each one of the six most important environmental variables independently (contribution > 5% to the model)

The threshold to map the occurrence likelihood was 0.502 obtained through the logistic threshold of equal training sensitivity and specificity. We defined three classes for mapping the probability: 1) below the threshold (<0.502), 2) the mean value between the threshold and the maximum value (0.502 – 0.661) and 3) above that mean value (>0.661) (Fig. 2b).

3.3. Factors affecting the badger road-kill events

We used a total of 508 road-kill records from which 407 presence records were used for training and 101 for testing (Fig. 1). The model produced an AUC of 0.834 which suggest that the model has a high performance and a good descriptor of badger mortality risk (Elith *et al.* 2011).

Road type was the variable that contributed more to the model (41.6%), followed by road sinuosity (31.5%) and distance to open areas (15%) (Table 2).

Highways seemed to increase the likelihood of badger vehicle-collision (Fig. 4). We also found a clear negative relation between road sinuosity and badger mortality risk. Road segments in the vicinity of open areas seemed to be related with higher risk of badger-vehicle collision.

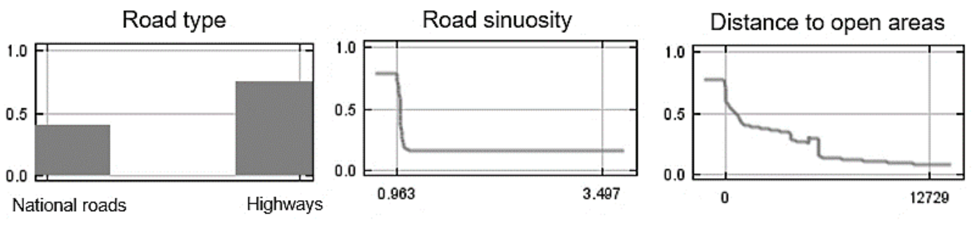

Fig. 4 Relationship between badger mortality risk and each one of the three most important environmental variables independently (contribution > 5% to the model)

The threshold value used to map the mortality risk was 0.454 obtained through the logistic threshold of equal training sensitivity and specificity. We defined three classes for mapping the probability: 1) below the threshold (<0.454), 2) the mean value between the threshold and the maximum value (0.454 – 0.680) and 3) above that mean value (>0.680) (Fig. 2c).

3.4. Spatial patterns of primary habitat and primary risk

When combining the three models we found different spatial patterns. While the badger setts model showed a high likelihood patch at north Portugal, the badger occurrence model did only show a few squares with high probability at the same region. We found that primary habitat areas were very much fragmented over Portugal, with some local concentrations at the centre (Estremadura, Ribatejo and Beira Interior regions) and south of Portugal (Alentejo region) (Fig. 5). The roads of southern of Portugal comprises several risky areas for badgers. Around 16% (15 912km^2) of the national territory comprises primary habitat for badgers while around 1% (214km) of the total road network comprises primary risk areas for badgers.

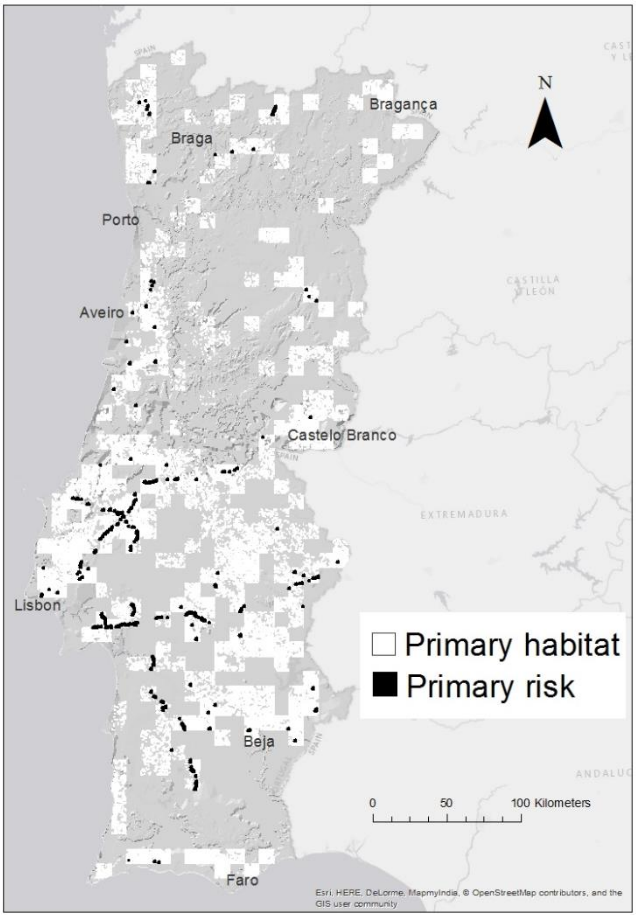

Fig. 5 Primary habitat and primary risk areas for badger

4. DISCUSSION

To our knowledge this is the first study to combine badger setts, occurrence and mortality data in order to identify the spatial patterns of primary habitat and primary risk for badger conservation. Badgers are generalists and its wide distribution makes it difficult to find a pattern of habitat selection. Surprisingly, our results show that the areas with primary habitat for badger are very fragmented. In general, we found that low proportion of arboreal cover and the presence of agricultural areas (<60%) are related with badger setts and badger occurrence, respectively. Regarding badger mortality risk, they seem to be more likely victim of vehicle-collisions at highways.

Our results of the analysis of badger setts suggest that the most important and the only significant feature for the selection of sett sites was the arboreal cover. The badger setts likelihood is unexpectedly higher in areas with low arboreal cover percentage. This in surprising because is commonly suggested that badgers select habitats with enough vegetation for shelter and protection of badger setts (e.g. Virgós and Casanovas 1999; Jepsen *et al.* 2005). In southern Europe in particular, several studies suggest that deciduous forests are a highly suitable habitat for badgers (e.g. Revilla and Palomares 2002; Rosalino *et al.* 2007; Santos and Beier 2008). An explanation for this negative relationship is the high amount of secondary setts at the analysis, that are assumed to be less important for badgers and therefore have more low habitat requirements (Roper 1994; Jepsen *et al.* 2005). We believe that the remaining variables were not significantly correlated with badger setts likelihood due to the small sample size. Nevertheless, we found that the probability of finding a badger sett is higher in areas with low proportion of open areas (as pastures, meadows or areas with sparse vegetation). These areas do not offer shelter for badgers and their cubs which are very active when young (Kruuk 1989; Neal and Cheeseman 1996). The positive selection of temporary cultures can be explained by the need to be close to food sources (Rosalino *et al.* 2005a). The positive relation (even not significant) with the presence of igneous plutonic ground is an unexpected result. Although badgers can use the gaps in the rocks or holes as setts (Lara-Romero 2012), several authors found higher preference for softer soils to construct their setts (Neal 1986; Doncaster and Woodroffe 1993; Hammond *et al.* 2001). This result may be incorrect since the badger setts survey was only performed at central Portugal, which may limit the availability of soil types. We also found that the likelihood of badger setts is low close to roads and streams, although not significant. Areas close to roads are obviously more accessible and exposed to human activities and badgers usually avoid disturbed areas for building their setts (Hammond *et al.* 2001) while areas closer to streams have higher risk of flooding and that may be an explanation for this avoidance (Hipólito *et al*. 2016). The low number of badger setts found provide some indications in terms of selection but unfortunately most of them were not significant.

In the analysis of the environmental factors that influence badger occurrence, the two most important variables were the presence of permanent cultures (negative relation) and the presence of sedimentary ground (positive relation). Mosaic habitats provide badgers complementary resources for their survival (Rosalino 2004) and that may be the reason of the pronounced negative relationship when the proportion of permanent cultures was above 60%. These areas comprise vineyards, orchards and olive groves which are important food sources for badger (consisting in 46% of its diet) (Rosalino 2004; Rosalino and Santos-Reis 2008; Requena-Muller *et al.* 2016). A high proportion of these cultures usually also mean high farming activities which may be an explanation for their tolerance until 60% of the area. The sedimentary soil seemed to be the most preferred type of soil by badger which is contrary to the badger setts analysis results. Such areas comprise sandstones, sand-sized minerals or rock grains and this preference can be explained by the need to build setts, which facilitate digging, besides being more efficiently drained (Neal 1972, 1986; Doncaster and Woodroffe 1993; Hammond *et al.* 2001). The third most important factor for the occurrence of badger was the temporary cultures (e.g. cereals, rice, potatoes or vegetables) with a positive relation until a proportion of 70%. These agricultural fields also correspond to additional food sources for badgers (Roper 1994; Rosalino 2004). In contrast to the badger setts results, the badger occurrence likelihood seemed to increase with the proportion of open areas. Although these areas do not provide enough shelter for construction of badger setts, they may represent good foraging spots as suggested by others studies in northern Europe (Kruuk *et al.* 1979; Hammond *et al.* 2001; Zabala *et al.* 2002; Elliott *et al.* 2015). These authors state that this preference is due to the high amount of earthworm's present at pastures, which is not considered an important food source for badgers in Iberia (they only feed from it when highly available) (Rosalino 2004; Rosalino *et al.* 2005a; Barea-Azcón *et al.* 2010). Nevertheless, Virgós *et al.* (2004) suggested that the earthworm's consumption by badger in some Mediterranean areas may be underrated. Similar to the badger setts analysis, the badger occurrence likelihood is low in the presence of high proportion of forests. Since 50% of national forests are covered with eucalyptus and coniferous plantations (CELPA

2015) badgers may avoid these areas due to the low amount of shrubs (Revilla *et al.* 2000), that do not provide neither shelter nor food.

The results of the mortality risk analysis suggest that the road segments more prone to badger-vehicle collisions are highways with low sinuosity and close to open areas. Highways represent high speed and in contrast to what was found by other studies with carnivores (Grilo *et al.* 2009, 2011; Grilo 2012), straight roads seemed to be highly related with the badger-vehicle collision likelihood. These studies reveal that high sinuosity represent less visibility for both driver and animal. However, low sinuosity may also represent high speed and less time to avoid collision. We found a higher probability of badger-vehicle collision close to open areas. An explanation is that these areas are very selected (for foraging) as shown at the badger occurrence analysis and therefore is comprehensible to occur more vehicle-collisions.

Our results show that the high quality habitats for badgers are concentrated mostly at the southern Portugal, some spots at the north and along the coastline. This scarce and fragmented pattern of primary habitat areas is surprising given that badgers are considered generalist in terms of habitat and food (Roper 1994; Wright *et al.* 2000; Virgós 2002; Rosalino *et al.* 2004). This pattern is similar to the one obtained by Santos-Reis *et al.* (2005) from a compilation of badger presences data (1985-2005). The highly risky areas are mostly located at the southern Portugal. They represent primary habitat with high road-kill risk which may turn these roads segments as ecological traps (Delibes *et al.* 2001; Naves *et al.* 2003; Battin 2004; Roever *et al.* 2013).

Although badger populations are not threatened and still common in Portugal, the loss of good quality habitats may lead to a fragmented distribution. The maintenance of natural Mediterranean forests together with some amount of agricultural fields (e.g. orchards and cereal fields) must be preserved for the long-term persistence of badger populations. Priority should be given to risky areas in terms of research (by validating the results with the estimation of road-kill rates) and of conservation (minimize the number of road-kill events by adapting the existing crossing structures or adding new wildlife passages; Grilo *et al.* 2008). Further research should be performed to determine whether the available primary habitat have an effect on populations viability over time.

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7. ANNEXES

Table A Summary of the 13 environmental variables estimated for the badger setts analysis in a scale of 500x500m^2

Category	Variables	Variables description	Units	Class	Source
Landscape	Open areas	Percentage of open areas (permanent pastures, meadows, beaches, sand dunes, bare rock and burned areas)	%	0 - 100	Cos2007, IGeoP
	Temporary cultures	Percentage of permanent cultures (vineyards, orchards and olive groves)	%	0 - 100	Cos2007, IGeoP
	Permanent cultures	Percentage of temporary cultures (rainfed, irrigation and rice paddies)	%	0 – 100	Cos2007, IGeoP
	Heterogeneous agricultural areas	Percentage of heterogeneous agricultural areas (temporary cultures and/or pastures associated with permanent cultures, agroforestry, mosaics with natural and semi-natural spaces)	%	0 - 100	Cos2007, IGeoP
	Forests	Percentage of forests (broad-leaved, coniferous or mixed, shrubs, natural herbaceous vegetation, sclerophyllous vegetation, open forests and clearcuts)	%	0 – 100	Cos2007, IGeoP
	Arboreal cover	Percentage of arboreal cover	%	0 – 100	Cos2007, IGeoP
	Distance to streams	Average distance to the nearest river or stream	M	56 – 5534	Agência Portuguesa do Ambiente, I.P.
Soil type	Sedimentary ground	Percentage sedimentary rock type	%	0 – 100	Agência Portuguesa do Ambiente, I.P.
	Metamorphic and sedimentary ground	Percentage of metamorphic and sedimentary rock type	%	0 – 100	Agência Portuguesa do Ambiente, I.P.
	Igneous plutonic ground	Percentage of igneous plutonic rock type	%	0 – 100	Agência Portuguesa do Ambiente, I.P.
	Floodable soils	Predominant presence of soils more willing to flood (1 - lithosols, regosols and fluvisols; 0 – others soils types) (Ferreira, 2000)	-	0/1	Agência Portuguesa do Ambiente, I.P.
Human pressure	Population density	Average number of habitants	Hab./ 0.25km^2	1 – 3105	GeoSTAT
	Distance to road	Average distance of the nearest road or street	m	88 – 6508	Digital Chart of the World

Table B Summary of the 16 environmental variables estimated for badger occurrence analysis in a scale of $10x10km^2$

Category	Variables	Description	Unit	Classes	Source
Topography	Altitude	Average altitude	m	0 – 1755	Agência Portuguesa do Ambiente, I.P.
Climate	Precipitation	Average annual precipitation	mm	1 - <400 2 - 400-800 3 - 800-1600 4 - 1600-2800 5 - >2800	Agência Portuguesa do Ambiente, I.P.
	Temperature	Average annual temperature	°C	1 - <7,5 2 - 7,5-12,5 3 - 12,5-17,5 4 - >17,5	Agência Portuguesa do Ambiente, I.P.
	Humidity	Average annual humidity	%	1 - <65 2 - 65-75 3 - 75-85 4 - >85	Agência Portuguesa do Ambiente, I.P.
Land use	Urban areas	Percentage of urban areas	%	0 – 100	Cos2007, IGeoP
	Open areas	Percentage of open areas (permanent pastures, meadows, beaches, sand dunes, bare rock and burned areas)	%	0 – 100	Cos2007, IGeoP
	Permanent cultures	Percentage of permanent cultures (vineyards, orchards and olive groves)	%	0 – 100	Cos2007, IGeoP
	Temporary cultures	Percentage of temporary cultures (rainfed, irrigation and rice paddies)	%	0 – 100	Cos2007, IGeoP
	Water bodies	Percentage of water bodies	%	0 – 100	Cos2007, IGeoP
	Heterogeneous agricultural areas	Percentage of heterogeneous agricultural areas (temporary cultures and/or pastures associated with permanent cultures, agroforestry, mosaics with natural and semi-natural spaces)	%	0 – 100	Cos2007, IGeoP
	Forests	Percentage of forests (broad-leaved, coniferous or mixed, shrubs, natural herbaceous vegetation, sclerophyllous vegetation, open forests and clearcuts)	%	0 – 100	Cos2007, IGeoP
Soil type	Sedimentary ground	Percentage sedimentary rock type	%	0 – 100	Agência Portuguesa do Ambiente, I.P.

	Metamorphic and sedimentary ground;	Percentage of metamorphic and sedimentary rock type	%	0 – 100	Agência Portuguesa do Ambiente, I.P.
	Igneous plutonic ground	Percentage of igneous plutonic rock type	%	0 – 100	Agência Portuguesa do Ambiente, I.P.
	Igneous volcanic ground	Percentage of igneous volcanic rock type	%	0 – 100	Agência Portuguesa do Ambiente, I.P.
Human pressure	Population density	Average number of habitants	Hab./ 100 km^2	0 – 156240	GeoSTAT

Table C Summary of the 12 environmental variables estimated for the study of badger road-kill events in a scale of 500x500m^2

Category	**Variables**	**Description**	**Unit**	**Classes**	**Source**
Road-related	Type of road	Type of road of each road segment (national roads - with one-way in each direction; highways - with more than one-way in each direction)	-	1 - national roads 2 - highways	Digital Chart of the World
	Intersections river-roads	Number of intersections between each road segment and rivers	-	0 – 4	Agência Portuguesa do Ambiente, I.P.
	Road sinuosity	Sinuosity index in each road segment (road length divided by shortest path length)	-	0.963 – 3.497	Digital Chart of the World
Landscape	Distance to urban areas	Average distance of each road segment to urban areas	m	0 – 6217	Cos2007, IGeoP
	Distance to open areas	Average distance of each road segment to open areas (permanent pastures, meadows, beaches, sand dunes, bare rock and burned areas)	m	0 – 12729	Cos2007, IGeoP
	Distance to permanent cultures	Average distance of each road segment to permanent cultures (vineyards, orchards and olive groves)	m	0 – 13026	Cos2007, IGeoP
	Distance to temporary cultures	Average distance of each road segment to temporary cultures (rainfed, irrigation and rice paddies)	m	0 – 7942	Cos2007, IGeoP
	Distance to water bodies	Average distance of each road segment to water bodies	m	0 – 17487	Cos2007, IGeoP

	Distance to heterogeneous agricultural areas	Average distance of each road segment to heterogeneous agricultural areas (temporary cultures and/or pastures associated with permanent cultures, agroforestry, mosaics with natural and semi-natural spaces)	m	0 – 6376	Cos2007, IGeoP
	Distance to forests	Average distance of each road segment to forests (broad-leaved, coniferous or mixed, shrubs, natural herbaceous vegetation, sclerophyllous vegetation, open forests, and clearcuts)	m	0 – 4172	Cos2007, IGeoP
	Landscape diversity	Landscape diversity index within a buffer of 500m for each side of the road segment, obtained through de Shannon-Weiner formula	-	0 – 1.84	Cos2007, IGeoP
Human pressure	Population density	Average number of habitants	Hab./ $0.25km^2$	0 – 141	GeoSTAT

Table D Summary of the 23 candidate models with the landscape, soil type and human pressure variables; AIC_c – second-order Akaike Information Criterion; $\Delta AIC_c=AIC_{ci} – AICc_{min}$; w_i – Akaike weight; bold the models with $\Delta AIC_c \leq 2$

Candidate models	**AIC_c**	**ΔAIC_c**	**w_i**
Landscape (11)			
Permanent cultures	104.85	6.34	0.00581
Heterogeneous agricultural areas	104.49	5.98	0.00695
Distance to streams	103.86	5.35	0.00953
Open areas	103.80	5.29	0.00982
Forests	103.17	4.66	0.01345
Temporary cultures	101.74	3.23	0.02750
Arboreal cover	**100.37**	**1.86**	**0.05455**
Arboreal cover + Temporary cultures	**100.42**	**1.90**	**0.05649**
Arboreal cover + Distance to streams	**100.32**	**1.80**	**0.05939**
Arboreal cover + Temporary cultures + Open areas + Distance to streams	**98.96**	**0.44**	**0.14354**
Arboreal cover + Open areas + Distance to streams	**98.59**	**0.07**	**0.15325**
Soil type (5)			
Sedimentary ground	104.65	6.14	0.00642
Igneous plutonic ground + Floodable soil	104.69	6.17	0.00668
Floodable soil	104.09	5.58	0.00849
Sedimentary and metamorphic ground	104.06	5.55	0.00862

Igneous plutonic ground	102.81	4.30	0.01610
Human pressure (3)			
Population density + Distance to road	105.67	7.15	0.00409
Population density	104.92	6.41	0.00561
Distance to road	103.72	5.21	0.01022
Landscape and Soil type (1)			
Arboreal cover + Open areas + Distance to streams + Igneous plutonic ground	**100.09**	**1.57**	**0.08130**
Landscape and Human pressure (1)			
Arboreal cover + Open areas + Distance to streams + Distance to road	**97.52**	**0.00**	**0.17859**
Soil type and Human pressure (1)			
Igneous plutonic ground + Distance to road	103.19	4.67	0.01414
Landscape, Soil type and Human pressure (1)			
Arboreal cover + Open areas + Distance to streams + Igneous plutonic ground + Distance to road	**99.78**	**1.26**	**0.11067**
Null model	103.97	5.45	0.00879

Table E Estimated coefficients (β), Standard error (SE), Z-test (z-value) and significance (p-value) for the best eight models of the GLM analysis of badger setts

Models	Variables	β	SE	z-value	p-value
Model 1	(Intercept)	0.28541	0.39996	0.714	0.4755
	Arboreal cover	-0.01600	0.00767	-2.087	0.0369 *
Model 2	(Intercept)	0.07482	-0.01413	0.175	0.8610
	Arboreal cover	-0.01413	0.00780	-1.812	0.0700 .
	Temporary cultures	0.03960	0.03064	1.292	0.1960
Model 3	(Intercept)	-0.11237	0.48383	-0.232	0.8163
	Arboreal cover	-0.01834	0.00804	-2.280	0.0226 *
	Distance to streams	0.00027	0.00018	1.445	0.1484
Model 4	(Intercept)	0.30809	0.53703	0.574	0.5662
	Arboreal cover	-0.02422	0.00882	-2.745	0.0060 **
	Distance to streams	0.00027	0.00019	1.420	0.1556
	Open areas	-0.08315	0.05012	-1.659	0.0971
Model 5	(Intercept)	0.11154	0.56010	0.199	0.8421
	Arboreal cover	-0.02235	0.00893	-2.502	0.0123 *
	Distance to streams	0.00026	0.00019	1.358	0.1745
	Open areas	-0.09058	0.05618	-1.612	0.1069
	Temporary cultures	0.04133	0.03285	1.258	0.2084
Model 6	(Intercept)	0.06477	0.60718	0.107	0.9151
	Arboreal cover	-0.02253	0.00900	-2.504	0.0123 *

	Distance to streams	0.00025	0.00019	1.365	0.1723
	Open areas	-0.08183	0.04929	-1.660	0.0968 .
	Igneous plutonic ground	0.00467	0.00544	0.857	0.3912
Model 7	(Intercept)	-0.02411	0.58782	-0.041	0.9670
	Arboreal cover	-0.02644	0.00919	-2.878	0.0040 **
	Distance to streams	0.00029	0.00019	1.554	0.1200
	Open areas	-0.08231	0.05168	-1.592	0.1110
	Distance to roads	0.00024	0.00016	1.497	0.1350
Model 8	(Intercept)	-0.34688	0.66973	-0.518	0.6045
	Arboreal cover	-0.02481	0.00935	-2.653	0.0080 **
	Distance to streams	0.00029	0.00019	1.514	0.1299
	Open areas	-0.07994	0.05054	-1.582	0.1137
	Distance to roads	0.00026	0.00016	1.589	0.1120
	Igneous plutonic ground	0.00569	0.00557	1.021	0.3073

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